Soil nutrient transformations in the rhizosphere via animal–microbial interactions

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Introduction

One of the major areas of interest in production ecology is in the realm of interactions and interfaces, both within and between ecosystems (Marshall, 1976; Coleman, Reid & Cole, 1983). Soils represent a particularly complex system of interactions. Thus, soil may be considered as a mosaic of various combinations of sand, silt, and clay, arranged in genetic horizons with their associated organic matter fractions and biota. As in many other systems, there are localized concentrations of organisms at microsites (aggregates or soil particles in general) as well as at larger sized interfaces such as that of leaf litter in soil and also between root and soil (Tisdall & Oades, 1982).

In a conceptual model (Fig. 2.1), there are discrete locations for existence, growth and activity of various organisms. Complex nutrient changes occur in which transformations from labile to stable, organic to inorganic may be principally controlled by microbial or faunal activities (Fig. 2.2). This paper will examine nutrient transformations, i.e. the initial uptake and immobilization by bacteria, fungi, and actinomycetes, and the subsequent release of the materials by other activities (mineralization) which are, to a considerable extent, mediated by the soil micro- and mesofauna.

Our objectives in this paper are threefold: (1) to examine principal animal–microbial–plant processes in ecosystems; (2) to present recent results of experimental microcosm studies; (3) to discuss impacts of these processes on community and ecosystem function.

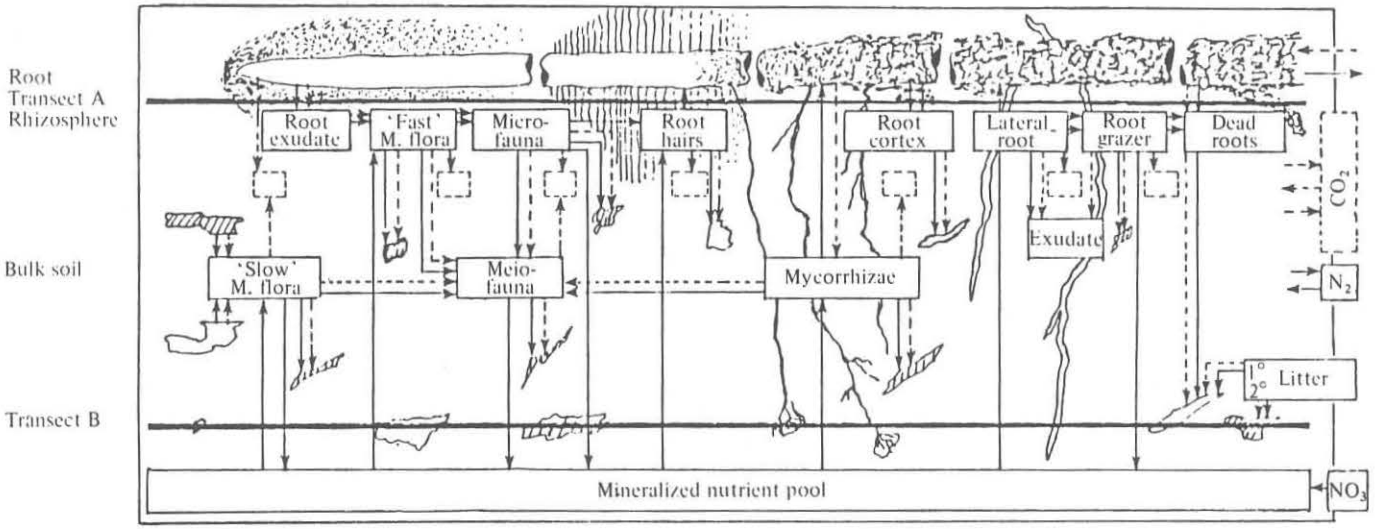


Fig. 2.1. Conceptual model of root in soil. Transect A (rhizosphere) shows structural features and interactions; transect B depicts the bulk (root-free) soil. (From Trofymow & Coleman, 1982.)

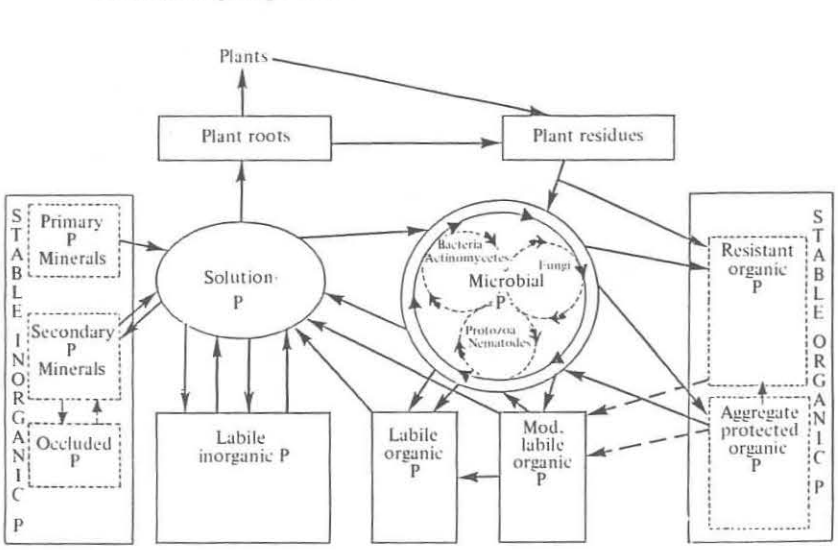


Fig. 2.2. Flows of stable and labile forms of inorganic and organic phosphorus in soil. Notice major flows into and out of solution P, regulated by microbial and faunal activity. (From Stewart & McKercher, 1982.)

Historical perspective

Microbial–faunal interactions

The history of investigations about the soil microflora and fauna contains much information on feeding, and distribution and abundance of microarthropods (Bornebusch, 1930; Jacot, 1940; Witkamp, 1960; Petersen, 1982), of protozoa (Cutler, Crump & Sandon, 1922; Stout, 1980), and of nematodes (Sohlenius, 1980; Yeates & Coleman, 1982). These studies emphasized feeding behaviour and followed the subsequent rise and fall of animal predator and microbial prey populations. In addition, the effects of fauna have been determined on total energy flow in populations and in communities, reviewed by Macfadyen (1968, 1969) and Luxton (1982). Energy dissipation during decomposition by the fauna is very minor compared to that contributed by the microflora. However, faunal effects on nutrient transformations and cycling within a community may be considerably greater than their contribution to simple energetics (Coleman, Reid & Cole, 1983; Clarholm, 1981). Hanlon (1981) found that rates of fungal respiration increased, peaked and then declined with increasing levels of collembolan grazing. Thus the effects of grazers appear to depend both upon their numbers and their activity. We will examine several aspects of direct effects such as feeding, which ruptures and lyses cells, and phoresy, the transport of various diaspores or propagules of microflora, as well as considering the more indirect effects of possible stimulation or altering of hormone production by various microorganisms.

Rhizodeposition studies

Historical reviews of rhizosphere chemistry and biology are ably presented by Darbyshire & Greaves (1973), Foster (1981), and Foster & Martin (1981). In considering the processes involving organic compounds in the rhizosphere in an ecological context, the term rhizodeposition (Shamoot, McDonald & Bartholomew, 1968) will be used.

Inputs to soil from the growing, maturing and senescing root have been placed in five categories (Fig. 2.3) (Rovira, Foster & Martin, 1979): (1) exudates, which are compounds of low molecular weight (MW), leaking from all cells into intercellular spaces or the soil; (2) secretions, low MW compounds released as the results of metabolic processes, not lost passively, as are exudates; (3) plant mucilages from a variety of sources, namely: the root cap, hydrolysates of primary cell wall polysaccharide, mucilages from epidermal cells with only primary cell walls (including root hairs), and mucilages from microbial degradation of outer multilamellate primary cell walls of old, dead epidermal cells; (4) mucigels, the heterogeneous array of polysaccharides including secondarily produced microbial polysaccharides (Jenny & Grossenbacher, 1963); (5) lysates, arising from autolysis of older epidermal cells when the plasmalemma fails. These will in turn provide a source of organic matter (OM) for microbial production and synthesis.

Estimates of rhizodeposition range from 30–50% (Coleman, 1976) to 60% (Lynch & Panting, 1980) of the total input of fibrous roots in a growing season. A detailed review of root mucilaginous substances and microorganisms associated with them (Chaboud & Rougier, 1981) also considers the major impacts which roots have on fixation of nitrogen by symbiotic and heterotrophic microbes, and on gaseous denitrification losses.

Rhizosphere organisms and plant growth factors

Several scientists in Europe and the USSR have suggested that bacteria, or bacteria and protozoa in combination, may produce hormones (IAA, gibberellins and/or kinetins) which markedly affect plant growth responses. Principal among these workers are Nikolyuk &

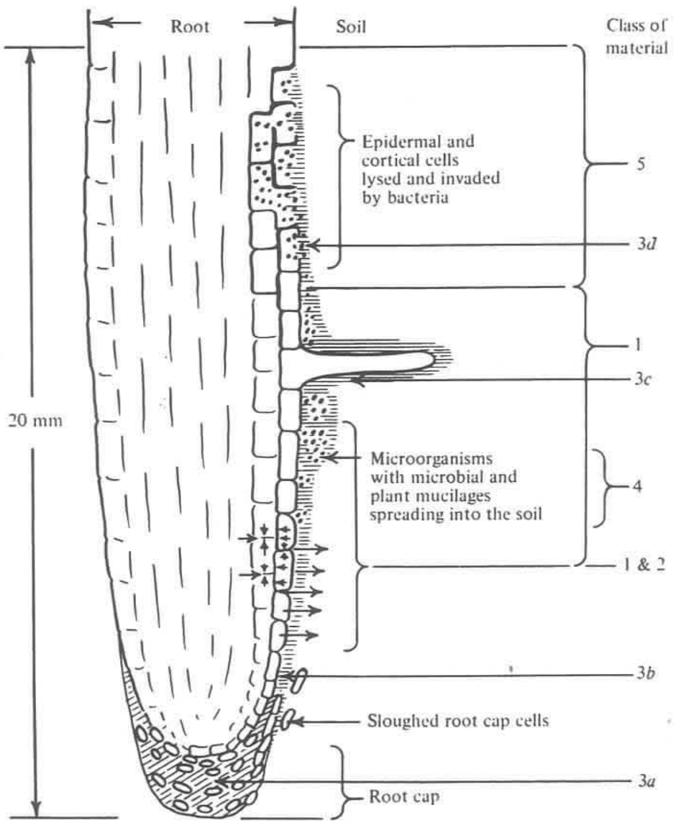

Root
Soil
Class of material
Epidermal and cortical cells lysed and invaded by bacteria
5
3d
1
3c
20 mm
Microorganisms with microbial and plant mucilages spreading into the soil
4
1 & 2
3b
Sloughed root cap cells
3a
Root cap

Fig. 2.3. Root growing in soil types of material entering soil: 1, exudates; 2, secretions from metabolic processes; 3, plant mucilages from various sources; 4, mucigels – a product of root–microbial components; 5, lysates from older root cells. (From Rovira, Foster & Martin, 1979.)

Geltzer (1972), who presented interesting data on field plots of cotton and flax in Uzbekistan SSR, where they measured growth increases of 10–30% in dry matter yields. The subject is reviewed in considerable detail by Brown (1975, 1976).

Another factor of considerable recent interest is the work on plant growth-promoting rhizo-microbes. Kloepper, Leong, Teintze & Schroth (1980*a*, *b*) and Schroth & Hancock (1982) have investigated fungal–bacterial interactions in several California field crops. They have suggested that certain plant growth-promoting bacteria have a marked inhibitory effect on other microbes, particularly pathogenic fungi. The postulated mechanisms of competition are complex, and centre on production of siderophores which compete for ferric iron in the rhizosphere. The subject is reviewed in more detail by Coleman *et al.* (1983).

Conceptual models of root–rhizosphere nutrient cycling

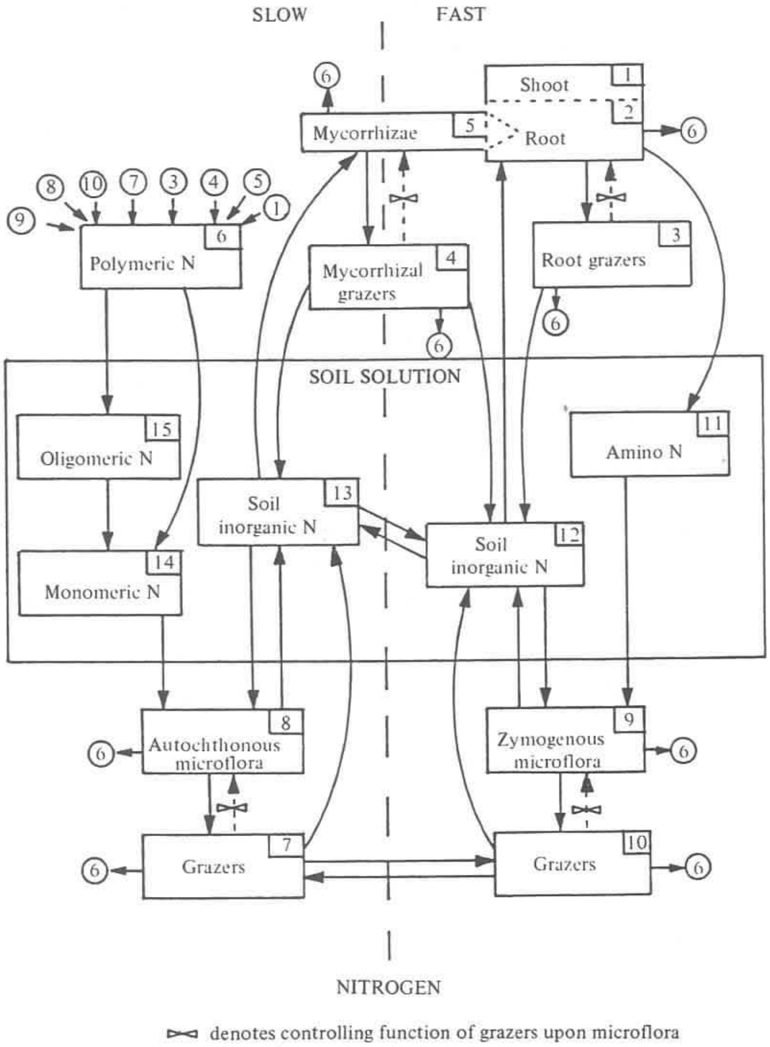
There have been two major pathways of decomposition and nutrient cycling postulated to occur in the root–rhizosphere region, and these have been termed 'fast' and slow' cycles (Anderson, Coleman & Cole, 1981). The fast cycle represents the release of low molecular weight carbon compounds such as amino acids and various mono- and oligosaccharides through root exudation or sloughing of cells. The more labile materials predominate in the rhizosphere region (Fig. 2.4) at or near the root tip. In comparison, the slow cycle is concerned with decomposition of less labile organic compounds such as those in cell walls or from partially decomposed root material or other sources of plant debris. This would include such substances as cellulose and lignin from plant cell walls, and polymeric nitrogen (chitin) present in arthropod exoskeletons, nematode eggs, and walls of many fungal hyphae. In both pathways, the microbes, with or without grazers, release some of the bound minerals such as nitrogen and phosphorus to the soil solution where they can be taken up by plants and microbes, and passed through other food chains. Mycorrhizae facilitate transport of certain nutrients, i.e. phosphorus, and perhaps nitrogen (Bowen & Smith, 1981), directly into the plant root.

Recent studies of nutrient cycling using microcosms

To investigate these phenomena further, we have looked at the effects on nutrient cycling of varying known components of soil microflora and micro- or mesofauna in the presence or absence of growing plants.

Nutrient cycling in the absence of plants

In early studies (Coleman *et al.*, 1977; Coleman *et al.*, 1978; Cole, Elliott, Hunt & Coleman, 1978) we examined microbial and faunal interactions in soil incubations without plants. These had known amounts of simulated root exudate added, and received gnotobiotic assemblages of bacteria (*Pseudomonas* sp.) and bacterial feeders. The experiments led us to some early conclusions about animal–microbial interactions. Both an amoeboid protozoan (*Acanthamoeba* sp.) and a bacterial feeding nematode (*Mesodiplogaster lheritieri*) increased system activity as measured by phosphorus and nitrogen mineralization (Woods *et al.*, 1982) as well as by carbon dioxide output in soil microcosms with a simple sugar (glucose) as the fast cycle carbon source. A more detailed analysis of the amoebal activity showed significant increase in release of inorganic P (bicarbonate-extractable phosphorus) with amoebae feed-



⋈ denotes controlling function of grazers upon microflora

Fig. 2.4. Conceptual model of nitrogen flow in soil systems showing labile components (right-hand side) and non-labile components (left-hand side). Decomposition products enter the soil solution for uptake by microbes (including mycorrhizae) and plant roots.

ing on the bacteria, in contrast to the ungrazed controls (Fig. 2.5). When the complexity of the system was increased by the interaction between omnivorous nematodes and amoebae, respiration was significantly greater in the more complex system in spite of decreased bacterial numbers (Fig. 2.6) (Coleman *et al.*, 1978). Calculations of production efficiency (production of grazer tissue)/(microbial tissue consumed) of the two grazers showed that the amoebae were four times more efficient at producing new body tissue than an equivalent biomass of bacterial-feeding nematodes. The subsequent loss of unlysed cells from the nematode guts may have had a significant feedback on early bacterial growth (days 2–5 of a 24-day incubation). This process is considered further later in this paper. The addition of ^{14}C-labelled glucose (Anderson, Elliott, Coleman & Cole, 1981) showed that the microbial grazing activity by the nematodes increased substrate utilization and nitrogen and phosphorus mineralization (Fig. 2.7). By returning nutrients to the soil solution, particularly in the first few days of the

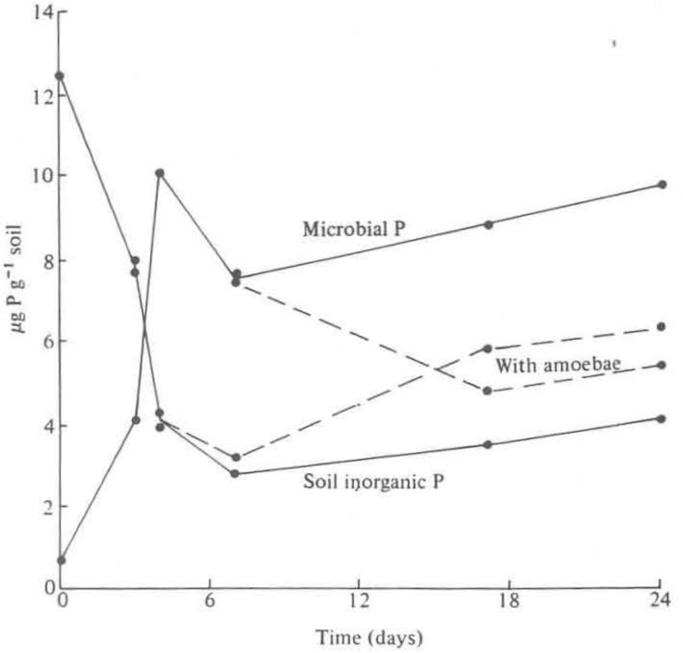


Fig. 2.5. Mineralization of microbial P in gnotobiotic microcosms with (– – – –) and without (————) amoebae (*Acanthamoeba polyphaga*). Rapid immobilization of soil inorganic P by day 7 is significantly reduced by amoebae feeding on bacteria (*Pseudomonas* sp.). (From Cole *et al.*, 1978.)

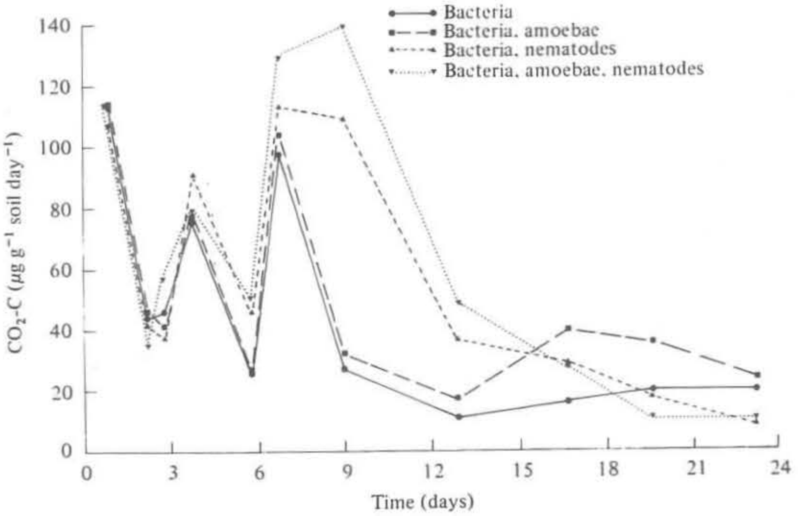


Fig. 2.6. Respiration in glucose-amended microcosms (200 μg glucose C g^{-1} soil added on days 0, 3, and 6). CO_2 output with bacteria and amoebae or nematodes is increased, with most marked enhancement between days 7 and 13 with two grazers in combination. (From Coleman *et al.*, 1978.)

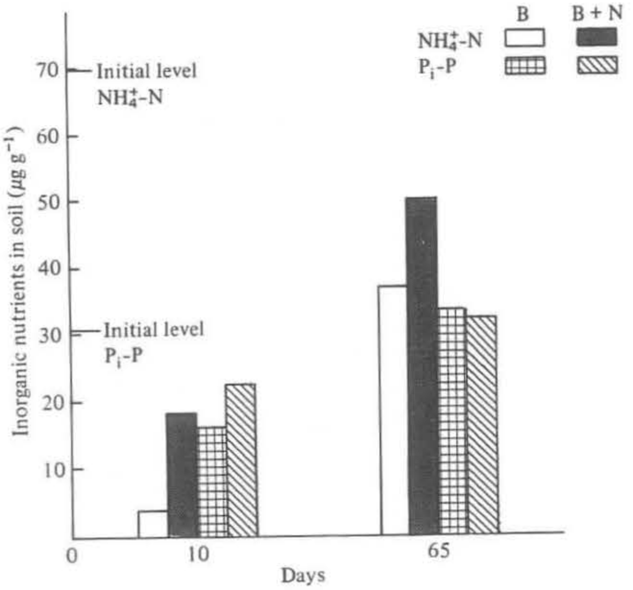


Fig. 2.7. Immobilization by bacteria alone, and subsequent return of NH_4^+-N and P_i-P in grazed systems (Day 10). Mineralization as per cent of ungrazed was greater on Day 10 than Day 65. B, bacteria; N, nematodes. (From Anderson *et al.*, 1981*a*.)

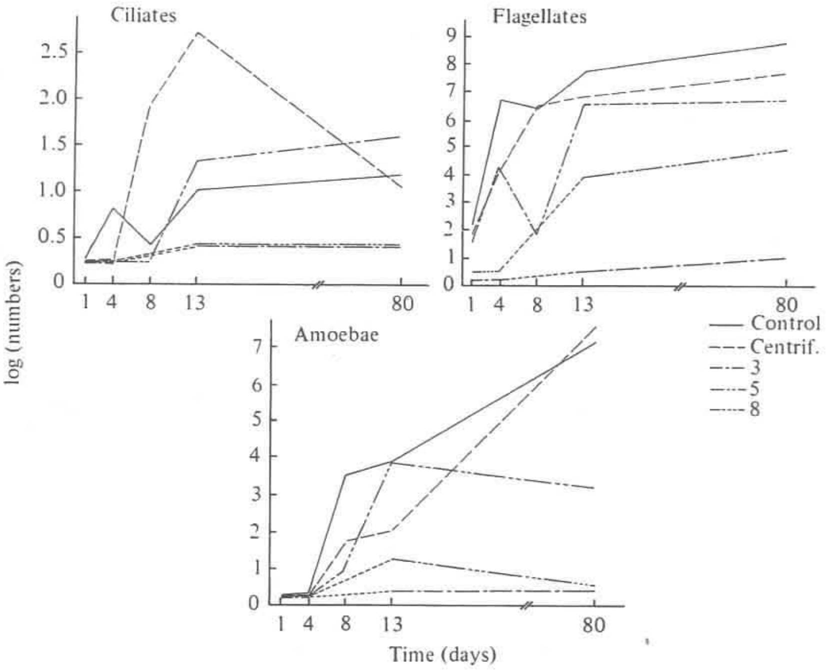


Fig. 2.8. Growth responses of ciliates, flagellates, and amoebae in soil microcosms receiving centrifuged, or 3, 5, and 8 μm filtrates of soil suspensions, or a complete mixture (control) of soil microbiota.

experiment, the microbivorous fauna maintained a somewhat higher metabolic activity, although total microbial biomass was less when grazed.

In other studies entire microbial and protozoan communities were manipulated via a selective filtration process using Nuclepore filters (McClellan, Frey, Campion & Coleman 1981). Changes were followed in respiration and nitrogen and phosphorus dynamics. Communities with several types of protozoa (ciliates, flagellates and amoebae, Fig. 2.8) and bacteria and fungi showed greater carbon and nitrogen mineralization (Figs. 2.9 and 2.10) than in those treatments which had only flagellates and a few amoebae. There was a corresponding decrease in bacterial populations (Fig. 2.11). The greatest increase in CO_2 was associated with the 8 μm filtration treatment, which also showed the largest number of grazing organisms but relatively fewer bacteria than the 3 μm and 5 μm filtrations. The 8 μm filtration also showed significantly more inorganic nitrogen as NH_4^+. In the 3 μm and 5 μm

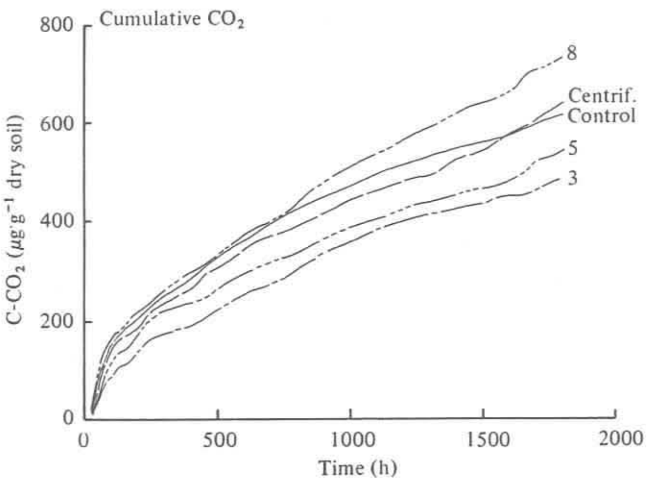


Fig. 2.9. Cumulative CO_2 output of microcosms with varying numbers of protozoa over the 80-day experiment of Fig. 2.8. Note the greater CO_2 output from the 8 μm treatment, with more amoebae.

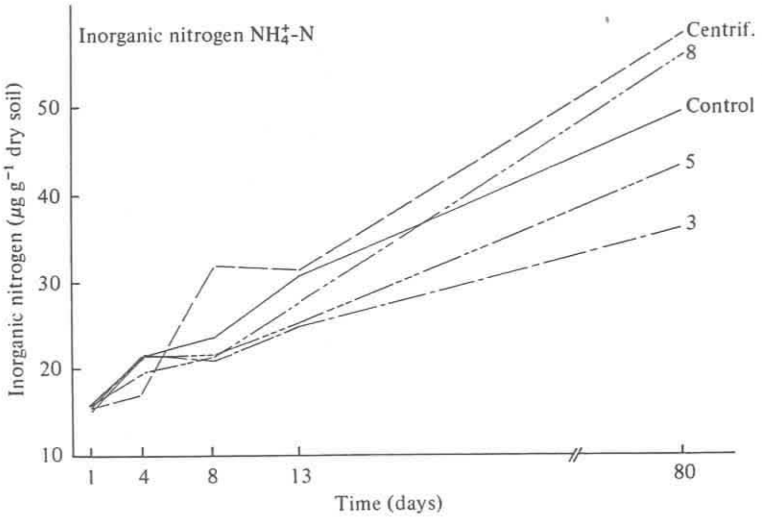


Fig. 2.10. Mineralization of NH_4^+-N in microcosms, with significantly more produced by day 80 of experiment in Fig. 2.8, 8 μm treatment.

filtrations with fewer grazers and relatively more bacteria the mineralization of nitrogen was commensurately decreased. Thus a greater species complexity shows greater turnover of nutrients than in simple incubations with one or two species.

In recent studies using more refractory substrates such as cellulose and chitin, mixed faunal systems often increased rates of decomposition and mineralization of nitrogen and phosphorus. Inoculation of high numbers of fungal-feeding nematodes into soil microcosms containing cellulose and a single fungal species decreased respiration rates, while soil inoculated with lower initial numbers had higher rates of respiration (Fig. 2.12) (Trofymow & Coleman, 1982). Bacteriophagic nematodes in cellulose and/or chitin-amended systems increased both rates of respiration and bacterial populations over those systems containing bacteria alone (Gould *et al.*, 1981; Trofymow & Coleman, 1982).

The method of feeding of the animals may govern the overall response. Bacterial feeders with a holophagic feeding mode release nutrients and, under certain conditions, eliminate considerable quantities of unharmed bacteria during periods of excess consumption (Smerda, Jensen & Anderson, 1971). In contrast, the stylet piercing of hyphae by a fungal-feeding nematode or other suctorial feeder immobilizes nutrients by leaving large portions of the fungi inactive or with empty cell walls. It remains to be seen whether fungal activity as measured by certain metabolic indicators such as fluorescein diacetate (Söderstrom,

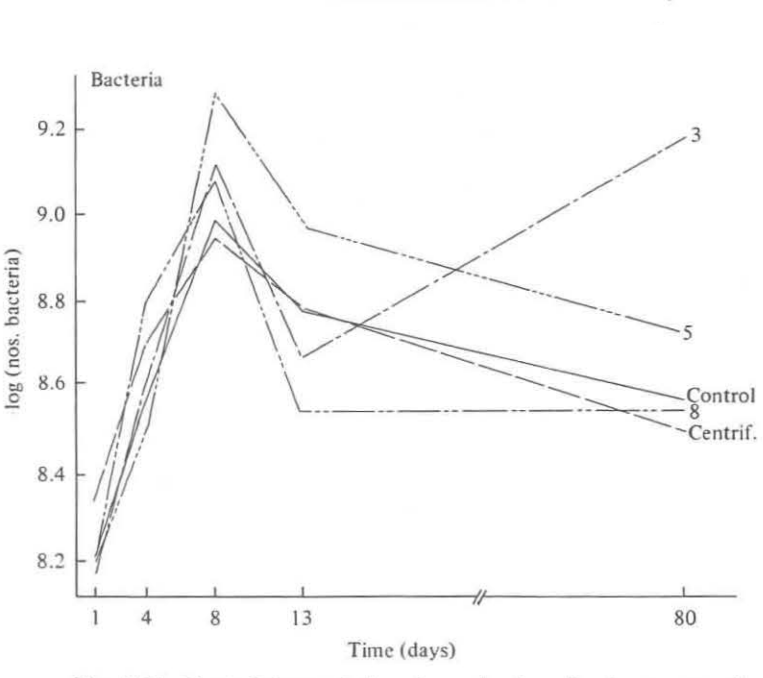


Fig. 2.11. Bacterial population dynamics in soil microcosms, showing reduction in numbers in 8 μm treatment, similar to that in control treatment (see Fig. 2.8), by 80 days.

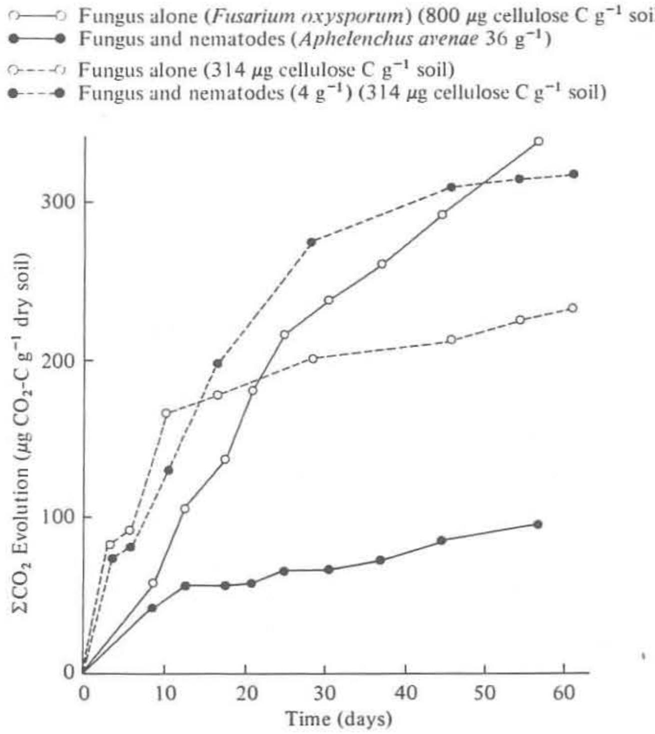


Fig. 2.12. CO_2 evolution from soil amended with cellulose and two levels of fungal-feeding nematodes. (Modified from Trofymow & Coleman, 1982.)

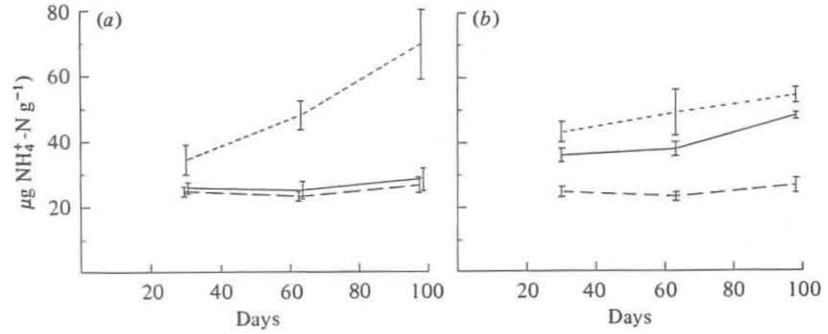


Fig. 2.13. Soil NH_4^+-N (mean and 95% confidence intervals) in soil amended with cellulose and chitin.
(*a*) Bacterial treatments: ——— uninoculated control; ——— bacteria alone (*Flavobacterium* sp.); ------- bacteria and bacterial-feeding nematode (*Pelodera* sp.). (*b*) Fungal treatments: ——— uninoculated control; ——— fungus alone (*Fusarium oxysporum*); ------- fungus and fungal-feeding nematode (*Aphelenchus avenae*). (From Trofymow & Coleman, 1982.)

1977; Ingham & Klein, 1982) would be a useful tracer to further identify the selective or more general feeding modes of some of the fungal feeders.

Nitrogen mineralization from a resistant organic nitrogen source such as chitin can be enhanced in systems containing microbial-grazing nematodes. Fig. 2.13 illustrates nitrogen mineralization in bacterial and fungal systems amended with cellulose and chitin. The additions of grazers in both systems increased levels of mineral nitrogen.

Increased rates of nutrient mobilization from organic matter via animal–microbial interactions may be especially important for plants growing in climatically stochastic environments such as shortgrass prairie and deserts. Since root extension and plant growth are heavily controlled by moisture, high rates of nutrient mineralization during moisture events would be critical for the plant.

Nutrient cycling in the presence of plants

Additional studies have been conducted showing the effects of animal–microbial mediated nutrient transformations in the presence of plants. Using seedlings of blue grama [*Bouteloua gracilis* (HBK) Griffiths] growing in microcosms, there was an increased ammonium nitrogen uptake in incubations containing bacteria and amoebae. Microcosms which received moderate (90 micrograms) or high (200 microgram) levels of ammonium nitrogen per gram of soil had significantly elevated plant tissue nitrogen levels when compared with those with plants and bacteria alone (Elliott, Coleman & Cole, 1979). The plant tissue nitrogen was twice that of controls (1.2 v. 2.4%) which had no amoebae grazing on bacteria. The experiment ran for approximately 45 days under less than optimal light conditions (*c*. 200–300 μE), and during this rather limited period there was no difference in net dry weight.

Additional studies growing blue grama (Ingham, Trofymow, Ingham & Coleman, unpublished) in larger microcosms (Trofymow, Gurnsey & Coleman, 1980) with a longer time span and higher light intensity have shown considerable increases in plant dry weight as well as nutrient uptake by the plant growing in the presence of various microbe-feeding nematodes. These experiments contained either bacterial- or fungal-feeding nematodes, and included purified chitin as a particulate organic nitrogen substrate added to soil low in inorganic nitrogen.

The bacteria and fungus inoculated into the soil were known chitin decomposers. Although plants growing in soil with bacteria grew more rapidly than plants in sterile soil, plants in microcosms inoculated with bacterial-feeding nematodes grew faster and had a higher nitrogen content than sterile plants or plants with bacteria alone (Fig. 2.14). Plants in soil with fungus and bacteria also had enhanced growth and nitrogen content over plants with only bacteria, but addition of fungal-feeding nematodes to the system had no significant effect. In a similar experiment in unamended soils (Ingham, 1981), the most vigorous plant responses were found in the most complex biological milieu, i.e. bacteria, fungi, bacterial-feeding nematodes and fungal-feeding nematodes (Fig. 2.15).

Discussion

Present options on the importance of the soil microfauna in enhancing decomposition are not unanimous. Bååth *et al*. (1978, 1981) measured growth of pine seedlings in soil and organic matter from field plantations of Scots pine (*Pinus silvestris*). The soils were acid and rather poor in nutrient with a carbon to nitrogen ratio of 44 : 1 in the humic material. With various members of the soil fauna (microarthropods, enchytraeids and protozoa) present, there was some enhancement of decomposition rate, but no significant increase in plant growth or in nutrient concentrations. They concluded that the fauna were not very important for nutrient return in the field. We suggest however that there might have been significant effects of mycorrhizae on nutrient uptake, as shown by Melin & Nilsson (1952) for ammonium uptake by ectomycorrhizae, but apparently this was not followed by the Swedish group.

Ingham (1981) found a considerable concentration of microbe feeding nematodes in the rhizosphere portion of the total soil, which one would expect to be areas of greater nutrient availability and turnover, particularly for high-energy carbon-containing compounds. At times he found as much as 20–40% of the total soil nematode populations in his microcosms in only 3% of the total soil, i.e. rhizosphere soil (Fig. 2.16). It therefore seems important in rhizosphere soil studies, especially with apparently suboptimal C : N ratios, to determine whether localized microsites with more favourable carbon to nitrogen ratios exist, and ascertain if only a small fraction of the total root system is needed to take up the majority of the nutrients required by the plant during the growing season. This sort of attention to spatial heterogeneity at the soil microsite level could lead to new insights in soil ecology. Sampling of bulk soil without distinguishing microsite regions, such as the rhizosphere, may dilute important interactions to an insignificant level.

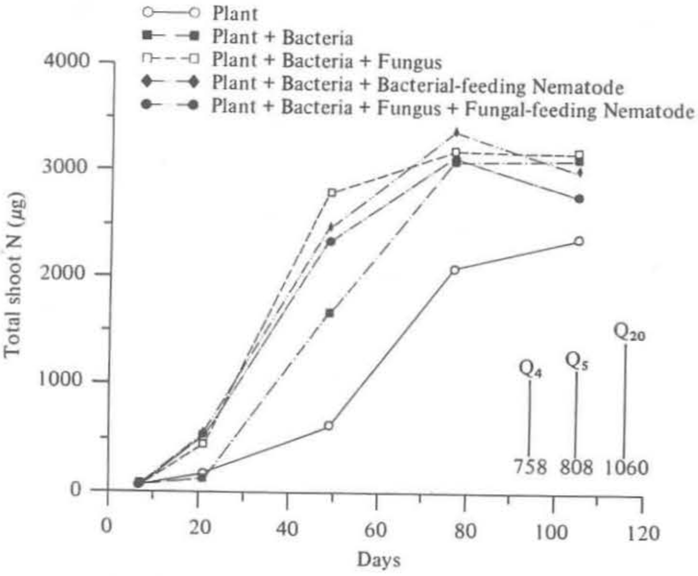


Fig. 2.14. Total shoot nitrogen in *Bouteloua gracilis* grown in chitin amended soil with different biological treatments. (From Ingham, Trofymow, Ingham & Coleman, unpublished.)

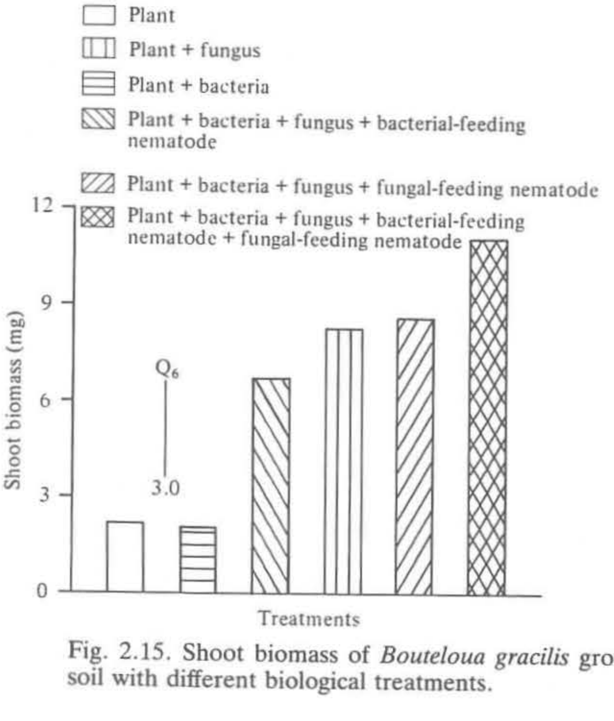


Fig. 2.15. Shoot biomass of *Bouteloua gracilis* grown in unamended soil with different biological treatments.

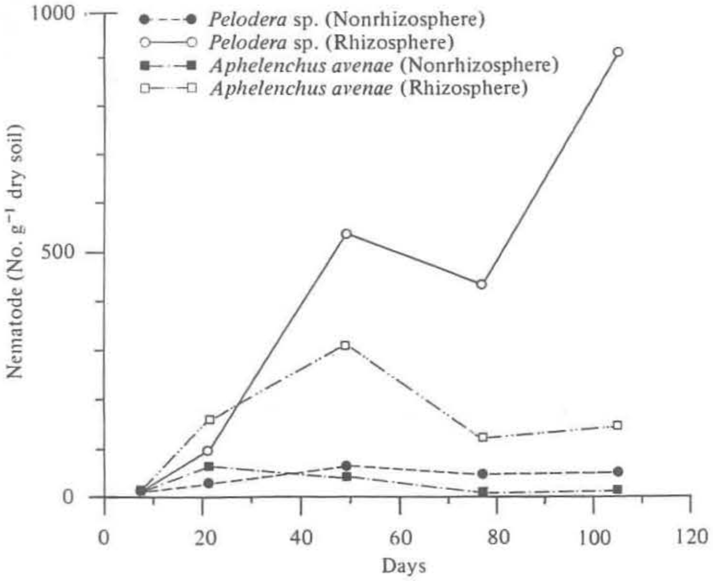


Fig. 2.16. Nematode populations in chitin amended soil from non-rhizosphere and rhizosphere areas of *Bouteloua gracilis*. (From Ingham *et al.*, unpublished.)

Faunal effects on microbial population dynamics

An important interaction between soil microflora and their respective grazers is the effect of the animals on the population sizes and turnover rates of the microflora. Most earlier studies have found that bacteriophagic nematodes significantly reduce bacterial numbers (Anderson *et al.*, 1981*b*; Coleman *et al.*, 1977, 1978; Whitford *et al.*, 1982), yet recently Abrams & Mitchell (1980) and Trofymow & Coleman (1982) have reported increases in bacterial numbers with bacterial-feeding nematodes compared to identical treatments without nematodes. Ingham and co-workers observed that these nematodes had no significant effect on bacterial population dynamics in non-rhizosphere soil. Yet in the rhizosphere, where bacterial and nematode population densities were much higher, bacterial-feeding nematodes significantly stimulated bacterial production (Fig. 2.17). Bacterial populations were also increased by the presence of a fungal-feeding nematode and this increase was, again, most marked in the rhizosphere.

Only a few studies have been carried out on effects of faunal feeding on root-associated, or mycorrhizal, fungi. Shafer, Rhodes & Riedel (1981) added the fungal-feeding nematode *Aphelenchus bicaudatus* to

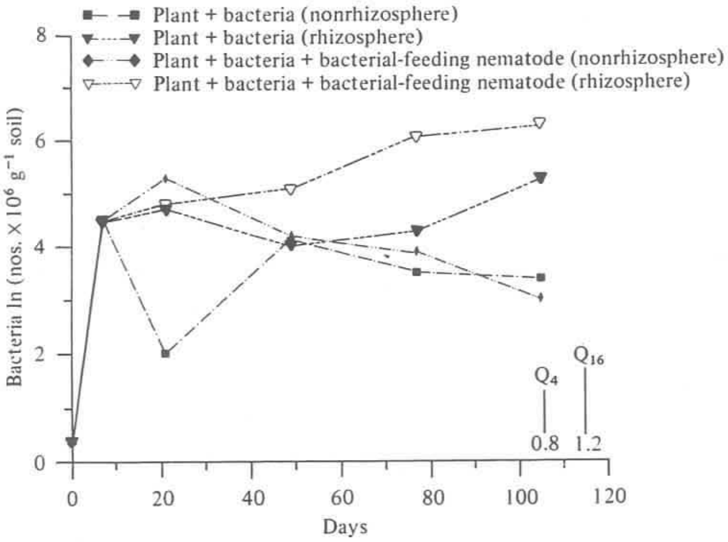


Fig. 2.17. Natural log of bacterial numbers in rhizosphere and non-rhizosphere soil of *Bouteloua gracilis* grown in chitin amended soil with and without *Pelodera* sp. (From Ingham *et al.*, unpublished.)

agar cultures of five species of ericoid mycorrhizal fungi. They observed destruction of aerial hyphae, and reduced mass of all species to half or two-thirds of control, ungrazed fungal cultures. Other workers (Hussey & Roncadori, 1981) have shown little or no effects of fungal-grazing nematodes on vesicular–arbuscular (VA) mycorrhizal biomass or subsequent plant growth. Further studies of nematode (including root-feeders)–mycorrhizal interactions are reviewed by Hussey & Roncadori (1982).

Information on microarthropod effects on mycorrhizal growth are even more scarce. Warnock, Fitter & Usher (1982) followed growth responses of *Allium porrum* in pots with and without the VA mycorrhizal fungus *Glomus fasciculatum*, and with and without the collembolan *Folsomia candida*. No direct feeding of the *Folsomia* was observed on external VA hyphae, but plant growth was significantly reduced in the plant–fungus–grazer pots than in those in which the Collembola were absent.

Recent work in our laboratory by John Moore and Robert Ames (unpublished) has shown consumption of hyphae and chlamydospores of several VA mycorrhizal fungi, in particular *Gigaspora rosea* and

Glomus fasciculatum, by the euedaphic collembolan *Onychiurus encarpatus*.

Microbe–faunal interaction effects on nutrient cycling

The more rapid cycling rate often observed in the systems which have feeding by predators upon microbial grazers may be very important to various primary producers. This is particularly true in systems having comparatively short (or episodic) pulses during the growing season, where nutrient availability may be critical over quite short time periods. Perhaps various lengths of food chains have differing effects on nutrient availability. The early work of Smith (1969) on even- and odd-numbered food chains should be considered in this context. He found that one-, three- and five-membered food chains had one sort of pattern (resources concentrated in the primary producer component), whereas those which had two, four, six or even-numbered members had a different primary control (greater activity of secondary predators, more free resources). These studies have been extended to terrestrial systems (Pimm & Lawton, 1977), including roles of omnivores (Pimm & Lawton, 1978).

Other studies in field systems have selectively removed active predatory forms (using biocides) that may play a role in enhancing or altering nutrient cycling. For example, the field studies of Santos & Whitford (1981), Santos, Phillips & Whitford (1981) and Elkins & Whitford (1982) may have some generality for soil systems. In plots with longer food chains, i.e. predatory mites feeding on bacterial-feeding nematodes, which in turn consumed bacteria in leaf litter bags in the Chihuahuan Desert of New Mexico, there was considerably greater litter decomposition, carbon dioxide evolution and nitrogen and phosphorus mineralization than in plots where the predatory mites were eliminated.

Implications and opportunities for future research

Trophic interaction processes, while important, are only a few of the many which occur in various terrestrial ecosystems. They should be viewed in the context of nutrient availability as well as short and long-term processes of organic matter formation and turnover. A small proportion, perhaps only 1 or 2% of the total soil organic matter is microbial (Jenkinson & Ladd, 1981), but a sizeable proportion of the total labile nitrogen and phosphorus is directly associated with that in the microbial pool. There are several experiments under way in various countries to examine the roles of soil fauna such as protozoa and nematodes in mineralization phenomena. This may be important in the standard ten-day incubation after treatment with ethanol-free chloroform (Jenkinson & Powlson, 1976).

There seem to be several similarities in the behaviour of roots, microbes, and fauna in using aggregations of organic matter as places in which to grow and proliferate. St John, Coleman & Reid (1983) have noted very similar behaviour of root growth and VA mycorrhizal growth in relation to soil OM. In each case, the roots and hyphae were distributed at random in open soil, then proliferated in small pockets (naturally occurring, or experimentally manipulated) of organic matter. The abundances of root and VAM closely approximated a negative binomial distribution.

A further aspect of interest is the apparent bi-directional flow of carbon in soil between roots on the one hand, and via gaseous loss of CO_2 on the other. Sparling, Cheshire & Mundie (1982) noted considerable microbial-derived CO_2 in barley root cell wall materials after seedlings grew in labelled organic matter for 42 days. These developments show that caution should be exercised in describing the extent of root–microbial–faunal interactions in soil systems.

We suggest that concentrating on localized areas of considerable activity within the mosaic of substrate types and pore space, such as the rhizosphere, will pay large dividends in further understanding the many processes which occur in soils, and will relate studies to a more holistic approach of nutrient cycling in entire ecosystems. Considering a whole spectrum of microflora, fauna, the plant root, and the soil abiotic physical substrate is likely to lead to important conceptual advances in this exciting area of ecology.

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